Systematic position and taxonomic level of grouse in the order Galliformes

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The clear division of the Galliformes (gallinaceous birds) into two groups—the ancient Cracoidea (Cracids and Megapodes) and the younger Phasianoidea—was established when the very first morphological revisions were made and, with rare exceptions (Clark 1960, 1964), has remained undisputed to the present day. The taxonomic status of these 2 groups varies from superfamily to suborder in the classifications proposed by different authors. Dividing the first group (Cracoidea) into the families Cracidae and Megapodiidae was an obvious course, as these differ morphologically and have long been widely separated geographically. The second group (Phasianoidea) differs clearly from the first (Cracoidea) in the position of the hallux on the tarsus, but its taxonomic subdivision is generally rather complex and much less straightforward. Up to the present day, various authors have argued with varying degrees of conviction for the inclusion in the Phasianoidea of the following groups: turkeys, guineafowl, peafowl, pheasants, Old World quails, New World quails and grouse. During the last 2 centuries, all possible combinations seem to have been tried in order to classify these groups, which have been variously given the rank of subfamilies within the single family Phasianidae, treated as separate families, or some united within the Phasianidae, others treated as independent families. However, the most usual classification has been that which treated as separate families the Phasianidae (comprising the subfamilies Odontophorinae, Perdicinae, Phasianinae, Numidinae), Meleagridae and Tetraonidae. New evidence has, however, now been produced which suggests that the guineafowl should be elevated to family rank (Sibley & Ahlquist 1990, Sych 1990).

The diversity of opinion with respect to classification of the Phasianoidea points above all to the low degree of divergence within the superfamily. It may further reflect the universal nature of phasianid morphology, which permits adaptation to a variety of environmental conditions. For example, the New World quails, despite having been separated longest from the main branch of phasianids (Sibley & Ahlquist 1990), have developed so few distinctions from the latter that they have been almost invariably treated by morphologists as only a subfamily within the Phasianidae. This case indicates that the quite considerable differences in DNA between the New World quails and other phasianids (more so than between guineafowl and other phasianids) are barely reflected in their morphology.

We have at least 2 methods for calculating the time of isolation of New World quails. One involves the use of starch gel electrophoresis with the fossil representatives of this group from the mid-Miocene in order to calibrate genetic distances (Gutiérrez *et al.* 1983). Another method focuses on geological and palaeogeographical data from roughly the time
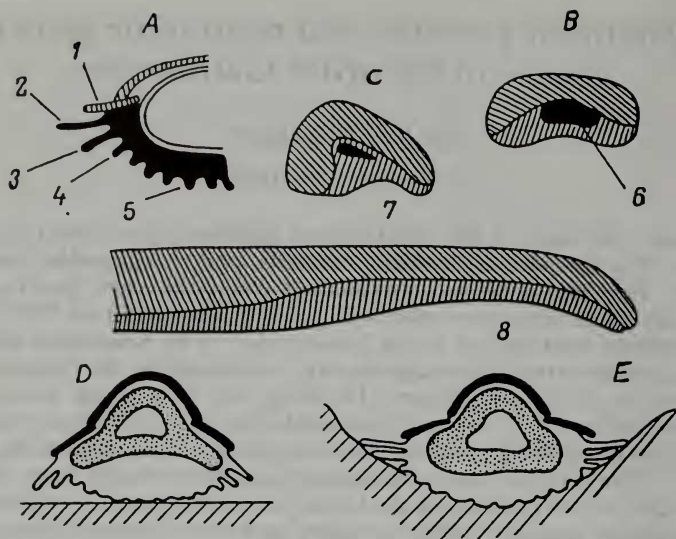
Figure 1. **Horny appendages on toes of grouse.** **A** = cross-section through terminal phalange of Capercaillie (*Tetrao urogallus*). 1 = lateral scutes; 2 = first row of appendages; 3 = second row of appendages; 4 = intermediate protuberance; 5 = foot papillae. **B** = transverse cross-section of growing appendage at its base; 6 = pulp. **C**: 7 = transverse cross-section of horny appendage; 8 = longitudinal cross-section of horny appendages. **D** = position of appendages when toe is in contact with branch. **E** = position of appendages when toe is in contact with snow. (From Potapov 1985.)

of the disjunction of North America and Europe. Interestingly, both methods give the same result: isolation in the lower Oligocene, c. 35 million years ago.

Based solely on DNA-hybridization data, Sibley & Ahlquist (1990) gave the New World quails the rank of family, the grouse that of sub-family. On the contrary, the grouse (which, like the turkeys, undoubtedly diverged much more recently than the New World quails—Sibley & Ahlquist 1990) show distinct morphological, ecological, ethological and, probably, also physiological differences, and we need to discuss the main features of this group separately.

Morphological characteristics of grouse

Pectinated toes

First we should consider a feature which is common to all grouse (with one exception) and not found in any other birds. This is the horny appendages (pectination) along the sides of the toes (Fig. 1). These appendages are shaped like miniature elongated scoops or nails with blunt tips. Forming a single or double row on both sides of the toes, they break and fall off in spring and regrow each autumn before the onset of winter. Only in the willow grouse and ptarmigan (genus *Lagopus*) which live in the most severe climatic conditions are these appendages replaced by

thick feathering; the pectination is found, nevertheless, in rudimentary form in one member of the genus *Lapogus*, the White-tailed Ptarmigan *L. leucurus* (in addition it has many relict features), thus giving a clear indication that the feathering of the toes is a secondary development, evolving in place of the appendages. The functional significance of the appendages, which appear only for the winter, is obvious: they more than double the surface area of the foot, which is an important aid not so much to locomotion on such a friable surface as snow (in most cases such walking on the snow is not necessary) as to the need to burrow into the snow 1–3 times per day to escape the severe winter cold. Each horny appendage acts as a miniature scoop, thereby significantly increasing the digging function of the foot and enabling any grouse to dig itself into the snow within a matter of seconds. Snow-burrows serve as thermal refuges where birds may spend most of the day during hard frost and where the temperature is constantly around -2 to $-3\,°C$ regardless of the ambient temperature. The very fact that lateral pectination of the toes is not found in any other avian taxon significantly increases the taxonomic value of this feature. Similar structures are found in some desert lizards inhabiting loose sand (e.g. *Phrynocephalus, Eremias*) (Buxton 1928), but these are not homologues of grouse pectination, but rather transformed scales.

Feathering of nostrils and toes

Another characteristic feature of grouse is the full and thick feathering of the nostrils and, perhaps as a consequence, the complete absence of the horny covering flap, the operculum; in some members of the Phasianidae (e.g. *Lerwa lerwa, Tragopan, Lophophorus, Tetraogallus*) there is some feathering around and on the surface of the operculum, but the operculum itself is not reduced.

In most grouse the tarsi are thickly feathered apart from a narrow strip along the rear side. The great majority also have lateral feathering extended to the base of the toes; in *Lagopus*, the toes are completely feathered, except for the upper part of the extreme tips. Many phasianids, especially northern or mountain species, have feathering on the upper part of the tarsus, but never extended to the lower third, still less to the toes.

Skeleton

Among special features of the skeleton, the most notable is the great width of the pelvis—more than 75% of its length (in phasianids, the maximum width is up to 75.8%), while its depth is only 16–17% of its length (as against 25–30% in phasianids). Such a sharp increase in pelvic width has resulted in a characteristic bend in the femur which in turn brings about a shift in the centre of gravity to place it above the foot when walking.

Musculature

There are no qualitative distinctions between the groups being compared, all are of a quantitative nature. The sole significant distinction— the absence in the grouse of the M. adductor digiti II (Hudson *et al.* 1959) has now lost its validity since the discovery that this muscle is lacking also

in a phasianid, namely the Tibetan Snowcock (*Tetraogallus tibetanus*) (Morioka 1975).

Digestive system

One of the main features of the digestive system is the exceptionally strong development of the caeca in all grouse species, this being most pronounced in members of the genus *Lagopus*. The length of grouse caeca is directly correlated with the length of the winter season and its relative severity, even within different populations of a single species. Generally, the length of the 2 caeca in grouse varies from c. 60 to 139% of the length of the small and large intestine; in phasianids, this ratio is usually up to 50%, in a few extreme cases up to 64% (Potapov 1985).

Among other peculiarities of the digestive system we should mention the absence in grouse of the gall bladder, which is so characteristic of other members of the Galliformes.

Ecological characteristics

Most important in this context as the main distinction from the phasianids is the peculiar food and feeding behaviour of grouse—their unique ability to survive on a monotonous plant diet throughout the severe winter season. Food items include twigs, buds, catkins and needles of various deciduous and coniferous trees and shrubs (e.g. *Betula, Alnus, Salix, Populus, Picea, Pinus, Abies*), i.e. a diet rich in cellulose and low in proteins and fats. However, food of this type is so abundant in northern forests that the birds need not spend much time or effort to obtain the required daily amount.

There are no fundamental differences between grouse and phasianids in respect of breeding strategy and timing (phenology), sex ratios, population dynamics, etc. The same general habitat types (open, bushy, forest, montane, etc.) are used by both groups, though grouse typically show a close link with forest and scrub vegetation and males of some species perform well-developed communal displays ('leks'). Open habitats invaded by grouse are primarily tundra (where some woody vegetation, even dwarf shrubs, is present), also to some extent steppe and semidesert, but never true desert. Grouse are found in all types of boreal forest, but have not penetrated into subtropical, still less tropical forests, the main reason being that their breeding range is confined within an area where there is a seasonal climate, with a pronounced winter period (snow cover, negative temperatures, short days).

Behavioural characteristics

The most remarkable feature of grouse behaviour is their ability to build snow-burrows as thermal refuges. For nocturnal or diurnal roosting, a bird uses vigorous movements of its bill and feet to dig a tunnel from 0.6 to 4 m long, at the end of which it makes a roosting chamber large enough to accommodate the bird comfortably, even with its feathers ruffled (Fig. 2). The depth of the chamber allows the grouse to stretch up and poke its head through the snow and look around before leaving its roost-hole. At moderate negative temperatures (minus 5 °C to minus 9 °C), grouse spend all the winter night in their burrows (Fig. 3),
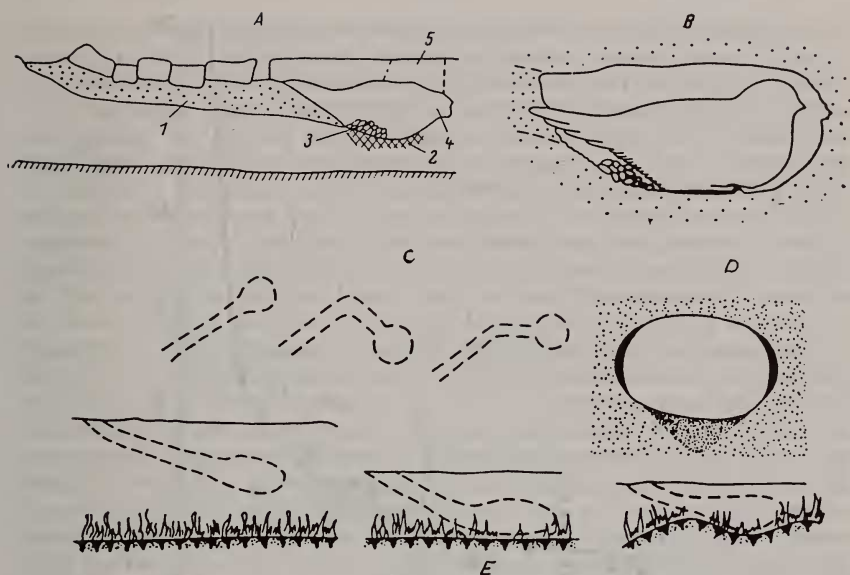
Figure 2. **Snow-burrow of grouse. A**=vertical cross-section of chamber; 1=tunnel blocked with snow; 2=platform of slightly thawed and compacted snow; 3=solid faeces; 4=signs of snow being eaten by bird; 5=future exit hole. **B**=position of bird in burrow. **C**=various types of tunnels. **D**=transverse cross-section of burrow (black indicates icing of walls, shaded area shows platform of slightly thawed and compacted snow). **E**=position of burrow at varying snow depths. (From Potapov 1985).

and if the temperature is lower, all night and most of the day as well. In exceptionally low temperatures, a grouse can spend up to 22 hours per day or even more than 2 days in succession in its snow-burrow roost.

Functional significance of the above-mentioned peculiarities

All the characteristic features of grouse described above are directly or indirectly related to survival in the northern winter season and represent a highly effective complex of adaptations which allow the birds to be year-round residents, with no recourse to migration. This complex of adaptations is based on the ability to survive the winter on plant food of low nutritional value, but available in abundance and at low cost in both time and energy. In its turn, this ability is based on the presence of well-developed caeca into which passes all the liquid digestive extract (chyme) containing the main nutritionally valuable substances (fat, protein, micro-elements), also some less useful, even poisonous, substances, extracted from buds, twigs, needles, etc. during the grinding process in the gizzard and their passage through the digestive tract. In the caeca, the extract undergoes treatment for not less than 24 hours (usually nearer 48 hours per portion), thus significantly prolonging the digestive process; otherwise, the passage of food through the alimentary canal without this delay in the caeca takes c. 4 hours. The chemistry of the
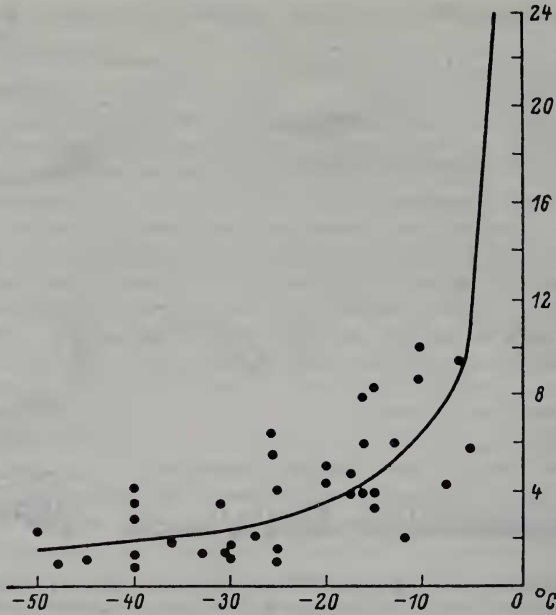
Figure 3. Time (Y-axis) spent outside the snow-burrow plotted against ambient temperature (X-axis). (From Potapov 1985.)

digestive process in the caeca requires further research; nevertheless, the caeca have been found to have intensive secretory activity with an exceptionally well-developed absorbent surface of their epithelium, the area and efficiency of which are considerably increased by the existence of well-developed ridges extending along the caeca. The caeca are thus a special kind of reactor working uninterruptedly throughout the winter to provide the bird with a constant supply of energy and nutrients.

It is on this main adaptation that all the other characteristic adaptations of tetraonid birds are based. They are able to survive on a diet of twigs, buds, catkins and conifer needles, i.e. items which are abundant and easy to obtain so that a minimum of time (30–90 minutes) needs to be devoted to gathering the daily ration. They have the ability to create thermal refuges under the snow which allow birds to regulate the ambient temperature by varying the time they spend in the burrow, which depends on the temperature outside. As a rule, the temperature in snow-burrows stays within optimal limits, just below 0 °C, and can even be regulated by the bird: if the temperature in the burrow rises above 0 °C and there is a consequent danger of the snow melting and the bird's plumage becoming wet, the grouse makes a small ventilation hole in the roof and the temperature in the burrow quickly drops. The thick feathering around the nostrils condenses moisture from the air exhaled by the bird, thus preventing the walls of the chamber icing up and an oxygen shortage arising. Any moisture is extracted from the faeces during their passage through the

large intestine so that they are solid and dry when excreted and add some warmth to the air in the snow-burrow, while also to some extent absorbing unwanted moisture and thus helping to counteract the danger of icing. The bird's thick tarsal feathering is a superb thermo-isolating mechanism, giving a protective mattress against the cold floor. The harder the frost, the drier the snow and the better its insulating quality. If a thaw sets in, the snow becomes wet and unsuitable for roosting, but the grouse anyway no longer has a need for such a refuge once the temperature is 0 °C or above. In general, staying in a burrow during low temperatures leads to a great saving in energy thanks to a sharp reduction in energy expenditure on thermoregulation (the lower limit of the thermoneutral zone for tetraonid birds is close to 0 °C) and the virtually complete absence of locomotion. The decrease in energy expediture for thermoregulation alone, even in a moderate frost of -20 °C, means that a grouse uses 20–35% less of the energy required to survive at the given temperature otherwise than in a snow-burrow. It is not surprising, therefore, that the strategically important adaptation of making snow-holes has led to the evolution of certain morphological features which so sharply distinguish grouse from the other Galliformes: pectinated toes, which greatly increase the digging ability of the feet when burrowing into snow; thick feathering around the nostrils which protects them from snow and reduces moisture produced by condensation of the exhaled breath; and thick tarsal feathering (extending to the toes in some species) which acts as an insulating layer between the bird's body and the floor of the snow-burrow.

Conclusions

The above descriptions present a general picture of how the whole complex of adaptations peculiar to grouse operates. These adaptations function only during the winter and enable birds to lead a sedentary life despite the marked seasonality of the climate. Gallinaceous birds have, through representatives of the grouse, colonized a completely new natural zone which came into being and evolved during the last geological epoch (the Pleistocene). This is the zone dominated by the boreal tree-shrub vegetation-type (both deciduous and coniferous), which is in turn well adapted to sharp seasonal changes in climate. The enormous area occupied by this zone embraces practically all the land surface of the Northern Hemisphere north of latitude 40 °N. In other words, the grouse occupy at least 40% of the whole range occupied by gallinaceous birds. For the relatively ancient Galliformes (Eocene epoch), the whole of the boreal zone was completely new, as the order had evolved in the tropics and subtropics and only a few representatives of families other than grouse eventually managed to pentrate into the southern margins of the boreal forest zone. In this connection, we should bear in mind the generally accepted principle that the wider the new adaptive zone, the higher the taxonomic rank of a group by the time it occupies the greatest part of the zone in question (Simpson 1969). All these reasons should encourage us to regard the grouse as a separate family within the suborder Phasianoidea.

All large taxa within this suborder (pheasants, partridges, New and Old World quails, peafowl, guineafowl, turkeys and grouse) differ one from another to varying degrees in a number of mainly morphological features and this doubtless reflects the complex structure of the suborder and varying speed of evolutionary processes. Qualitatively and quantitatively the most distinctive groups are the grouse and guineafowl. However, while the grouse have predominantly new evolutionary features, the guineafowl are a distinctly archaic group. It is quite possible that the guineafowl also merit separation as an independent, but extremely primitive family, approaching in a number of morphological features, the suborder Cracoidea (Sych 1990).

Deserving of special attention are the New World quails whose morphology has not allowed taxonomic rank higher than subfamily within the Phasianidae. However, DNA-hybridization data have demonstrated that this group separated from the main branch of phasianids 35–65 million years ago, and should therefore be given family rank (Sibley & Ahlquist 1990, Sibley & Monroe 1990). It should be noted, incidentally, that determining the time when the New World quails diverged from the other phasianids can be done without recourse to the DNA-hybridization method, but instead by using palaeogeographical data from the time when the European and American continents separated. The DNA-hybridization results merely show the divergence of the chromosome structures; but in the present case it is clear that there is no corresponding divergence in the morphology of the groups being compared. This kind of dichotomy is by no means rare, having arisen regularly in recent times. In the case under investigation, it is my firm conviction that preference should be given to a judgement based on morphological criteria as these most convincingly show the results of the process of evolution. In assessing the taxonomic level of grouse, we therefore give higher priority to morphological features, their adaptive (functional) significance and specificity of ecological niches. On this basis, the relatively young, but morphologically and ecologically distinct grouse undoubtedly merit family rank within a superorder Phasiani, while the much older New World quails, which show no significant distinctions from the partridge and quails of the Old World (despite having separated millions of years ago), should be treated as a subfamily within the Phasianidae. The guineafowl, which are also younger than the ·New World quails, but (unlike grouse) are distinguished by their predominantly archaic features, suggesting a close relationship with the suborder Cracoidea, should evidently also be given family rank (Sych 1990).

The results of the process of evolution are not dependent simply on time, nor is taxonomic rank a mere function of time; it can be determined only after a detailed and comprehensive investigation of morphological, ecological and ethological features.

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